# NICHE PARTITIONING IN *DOWNINGIA BELLA* AND *D. CUSPIDATA* (CAMPANULACEAE) IN THE VERNAL POOLS OF THE SANTA ROSA PLATEAU PRESERVE, CALIFORNIA

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### Abstract

*Downingia bella* and *D. cuspidata* were sympatric in 10 of 13 study pools. Of the three pools where they were allopatric, two pools were relatively shallow, dried up early, and contained only *D. cuspidata*. In pools where the species were sympatric, flowering of *D. bella* was correlated positively with pool depth, whereas flowering of *D. cuspidata* was correlated negatively. Peak flowering periods of *D. bella* usually occurred 2–4 weeks later than *D. cuspidata*. *Downingia bella* was significantly larger than *D. cuspidata* for seven morphological characters measured. Pollinators of *D. bella* were primarily *Bombus californicus* and *B. sonorus*. *Downingia cuspidata* was visited by numerous insect species, but neither species of *Bombus* was observed. Niche partitioning of the two *Downingia* species, which are sympatric in most of the vernal pools on the Santa Rosa Plateau, was demonstrated through differences in distribution, flowering phenology, morphology, and pollinators.

*Downingia* is a genus of semi-aquatic annual plants (Campanulaceae: subfam. Lobelioideae). Fourteen species of *Downingia* are distributed in western North America and in South America in ephemeral aquatic habitats (Weiler 1962). Thirteen species occur in North America with six of these indigenous to California. In South America there are two species, one of which occurs in both California and Chile. Most species of *Downingia* are restricted to vernal pools (Weiler 1962). When these seasonal habitats begin to dry up in the spring, growth of *Downingia* is rapid and masses of blue or purple flowers are produced from thousands of plants.

The presence of two or three sympatric *Downingia* species in many vernal pools (Weiler 1962, Lin 1970, Foster 1972, Rickabaugh 1974, Macdonald 1976, Holland and Jain 1977, 1984, Gunn 1982, Schlising and Sanders 1982) indicates that there are considerable niche similarities between species. Holland and Jain (1981) found that niche partitioning in vernal pools occurs largely at the level of genera, with species replacing each other along a regional pattern. There are several regions with overlapping ranges of two or more species of *Downingia,* but "true" sympatry was found in less than 10% of the vernal pools in California (Holland and Jain 1977). *Downingia bella* Hoov. and *D. cuspidata* (Greene) Greene (Figs. 1, 2) are found sympatrically in many vernal pools at different locations in California (Holland

FIGS. 1, 2. *Downingia* corollas. 1. *Downingia bella,* ×2. 2. *Downingia cuspidata,* ×2.

and Jain 1977, Lathrop and Thorne 1983). Both species have protandrous, resupinate flowers, bilocular ovaries, haploid chromosome numbers of 11, and are indigenous to California (Weiler 1962). *Downingia bella* differs from *D. cuspidata* in having three dark pur-
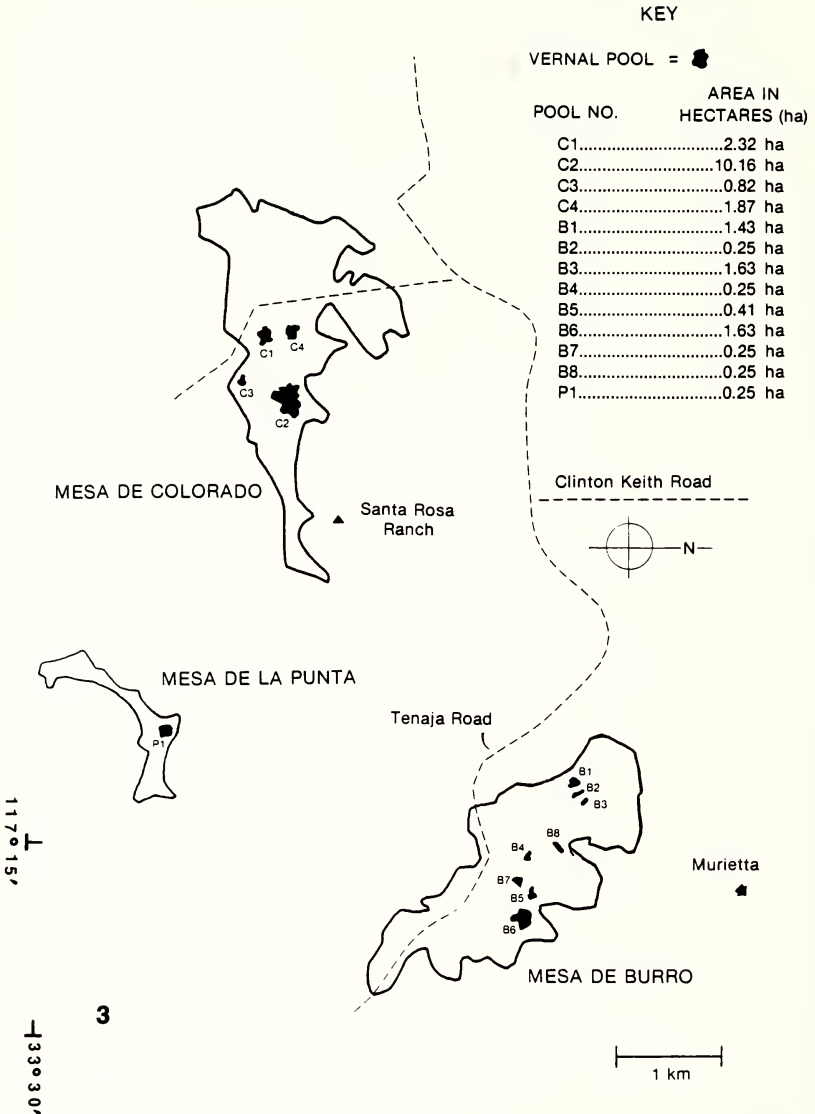
KEY

VERNAL POOL =

| POOL NO. | AREA IN HECTARES (ha) |
|---|---|
| C1 | 2.32 ha |
| C2 | 10.16 ha |
| C3 | 0.82 ha |
| C4 | 1.87 ha |
| B1 | 1.43 ha |
| B2 | 0.25 ha |
| B3 | 1.63 ha |
| B4 | 0.25 ha |
| B5 | 0.41 ha |
| B6 | 1.63 ha |
| B7 | 0.25 ha |
| B8 | 0.25 ha |
| P1 | 0.25 ha |

MESA DE COLORADO

C1  C4
C3
C2

Santa Rosa
Ranch

Clinton Keith Road
- - - - - - - - - - - - - - -

—N—

MESA DE LA PUNTA

P1

Tenaja Road

B1
B2
B3

B8
B4
B7
B5
B6

Murietta

MESA DE BURRO

117° 15'

3

33° 30'

1 km

FIG. 3.  Distribution of vernal pools on three mesas of the Santa Rosa Plateau Preserve. Map used by permission of *Aliso.*

ple spots at the corolla throat, indehiscent fruits, and longitudinally striate seeds.

The objective of this study was to test distribution, phenology, morphology, and pollination of *Downingia bella* and *D. cuspidata*

to determine if these species occupy different niches when they are sympatric.

## STUDY AREA

Field work for this research was conducted in the spring and summer of 1982 in the vernal pools of the Santa Rosa Plateau Preserve (Lathrop and Thorne 1985a) located on the Santa Rosa Plateau (Lathrop and Thorne 1985b), Riverside County, California. Thirteen vernal pools are located on three lava-capped mesas; eight on Mesa de Burro, four on Mesa de Colorado, and one on Mesa de la Punta (Fig. 3). Pool sizes, including the zone of influence around each pool, range from 0.25–10.16 ha (Fig. 3). *Downingia bella* and *D. cuspidata* occur sympatrically in 10 of the 13 pools (Lathrop and Thorne 1983).

## METHODS

*Distribution.* Intrapool distribution, flowering frequency (%), relative abundance (%), and plant density (n/m²) of *D. bella* and *D. cuspidata* were determined from quadrat measurements at various times throughout the 1982 season in pools B1, B5, B6, C1, C2, C3, and C4 (Fig. 3). Belt transects (0.3 × 1.8 m), marked off into 24 quadrats (225 cm²), were placed perpendicular to a radius of each of the seven pools at regular intervals along 7–15 transect lines running from the edge to the center of the pool. All quadrats, at a particular distance from the edge of the pool, were summed together to get flowering frequency (%) and mean plant density (n/m²) at that distance. At each placement of the belt transect, all 24 quadrats were measured for flowering frequency, and three randomly selected quadrats were measured to determine plant density (n/m²). The plane-table method (Compton 1962) was used to survey pools B1 and C2 for pool depth profiles. Depth profiles for all the remaining pools measured were taken from Stagg and Lathrop (1984). Weekly surveys of the 13 vernal pools were conducted between April and September 1982 to determine presence, relative abundance, and distribution in the different vernal pools through time. Linear correlation was used to analyze the relationship of the flowering frequency of *D. bella* and *D. cuspidata* with pool depth. Because flowering was nearly simultaneous throughout the pool in pools B1, B6, C1, C3, and C4, linear correlation was analyzed one date only. Flowering occurred in temporal bands following the receding water in pools B5 and C2. Pool depth was compared with highest frequency of flowering for both species on three different dates in these pools.

*Flowering phenology.* Data from weekly surveys and quadrat measurements were used to analyze the flowering phenology of *D. bella*

TABLE 1. RELATIVE ABUNDANCE (%) AND THE SEASON'S HIGH MEAN ($\bar{x}$ ± s.d.) DENSITY (n/m²) OF *Downingia bella* AND *D. cuspidata* IN 13 VERNAL POOLS OF THE SANTA ROSA PLATEAU PRESERVE, CALIFORNIA. Relative abundance was determined from quadrat data (B1, B5, B6, C1, C2, C3, C4) and from count data (B2, B3, B4, B7, B8, P1). K = number of 225 cm² quadrats.

| | Relative abundance | | | | High mean density | | | |
| | D. bella | | D. cuspidata | | D. bella | | D. cuspidata | |
| Pool | n | % | n | % | K | n/m² | K | n/m² |
|---|---|---|---|---|---|---|---|---|
| B1 | 3824 | 55 | 3159 | 45 | 24 | 237 ± 191 | 24 | 152 ± 218 |
| B2 | 1075 | 72 | 410 | 28 | | | | |
| B3 | | | 1201 | 100 | | | | |
| B4 | 4 | 12 | 29 | 88 | | | | |
| B5 | 638 | 11 | 5359 | 89 | 30 | 18 ± 46 | 30 | 406 ± 384 |
| B6 | 89,154 | 93 | 6291 | 7 | 21 | 351 ± 216 | 21 | 233 ± 182 |
| B7 | | | 1812 | 100 | | | | |
| B8 | 69 | 20 | 269 | 80 | | | | |
| C1 | 2592 | 74 | 931 | 26 | 36 | 41 ± 37 | 36 | 92 ± 189 |
| C2 | 182,710 | 81 | 43,068 | 19 | 30 | 356 ± 260 | 30 | 350 ± 352 |
| C3 | 527 | 15 | 7407 | 85 | 36 | 30 ± 88 | 36 | 221 ± 197 |
| C4 | 7 | <1 | 1635 | >99 | 30 | 1 ± 8 | 30 | 65 ± 61 |
| P1 | 1 | 100 | | | | | | |

and *D. cuspidata.* Peak flowering for each pool was designated as a two week period when flowering plants were at their highest frequency or abundance. The inundation/desiccation condition of the vernal pools was noted throughout the season during weekly surveys. Desiccation dates were recorded when pool beds became dry and hard. Linear correlation was used to compare the peak flowering periods for *D. bella* and *D. cuspidata* with pool desiccation dates.

*Morphology.* Seven morphological characters were measured. From pools B6 and C2 where the two species were sympatric, mature sample specimens of *Downingia bella* (n = 40) and *D. cuspidata* (n = 36) were collected at random, pressed, dried, and taken to the lab for measurements. Parameters measured for each specimen and flower were: 1) linear measurements of plant height, and leaf, ovary, sepal, and tube length; 2) number of flowers per plant; and 3) number of open flowers per plant. One-way ANOVA was used for statistical comparison of these morphological parameters.

*Pollination.* During weekly surveys, 10 minute observations were made at each pool that contained both species. Insects visiting each species were observed and specimens collected. Chi-square contingency analysis was used to compare the visitation frequency of two of the pollinators (*Bombus californicus* and *B. sonorus*) on both *Downingia* species.

<div align="center">RESULTS</div>

*Interpool distribution. Downingia bella* and *D. cuspidata* were found sympatrically in 10 of the 13 vernal pools of the Santa Rosa Plateau Preserve (Table 1). In the remaining three pools, *D. cuspidata* was found exclusively in two pools, whereas *D. bella* was found exclusively in only one. Although pool C4 had both species present, it mostly contained *D. cuspidata. Downingia cuspidata* was dominant in five of the 10 sympatric pools. *Downingia bella,* however, was four times more abundant than *D. cuspidata* when all pools were totaled (Table 1). This high relative abundance was due to the dominance of *D. bella* in four of the five largest vernal pools on the plateau.

*Intrapool distribution.* Intrapool flowering frequency patterns varied considerably for both species (Figs. 4–7). In some pools, flowering was nearly simultaneous throughout the entire pool (Figs. 4, 6, 7). Other pools exhibited temporal flowering bands that followed the receding water (Fig. 5). Despite this variability, there was a spatial segregation of the two species in all the pools. While one species increased in flowering frequency, the other decreased. In all pools except pool C4, *D. bella* reached its highest flowering frequency towards the center of the pool, whereas *D. cuspidata* reached its
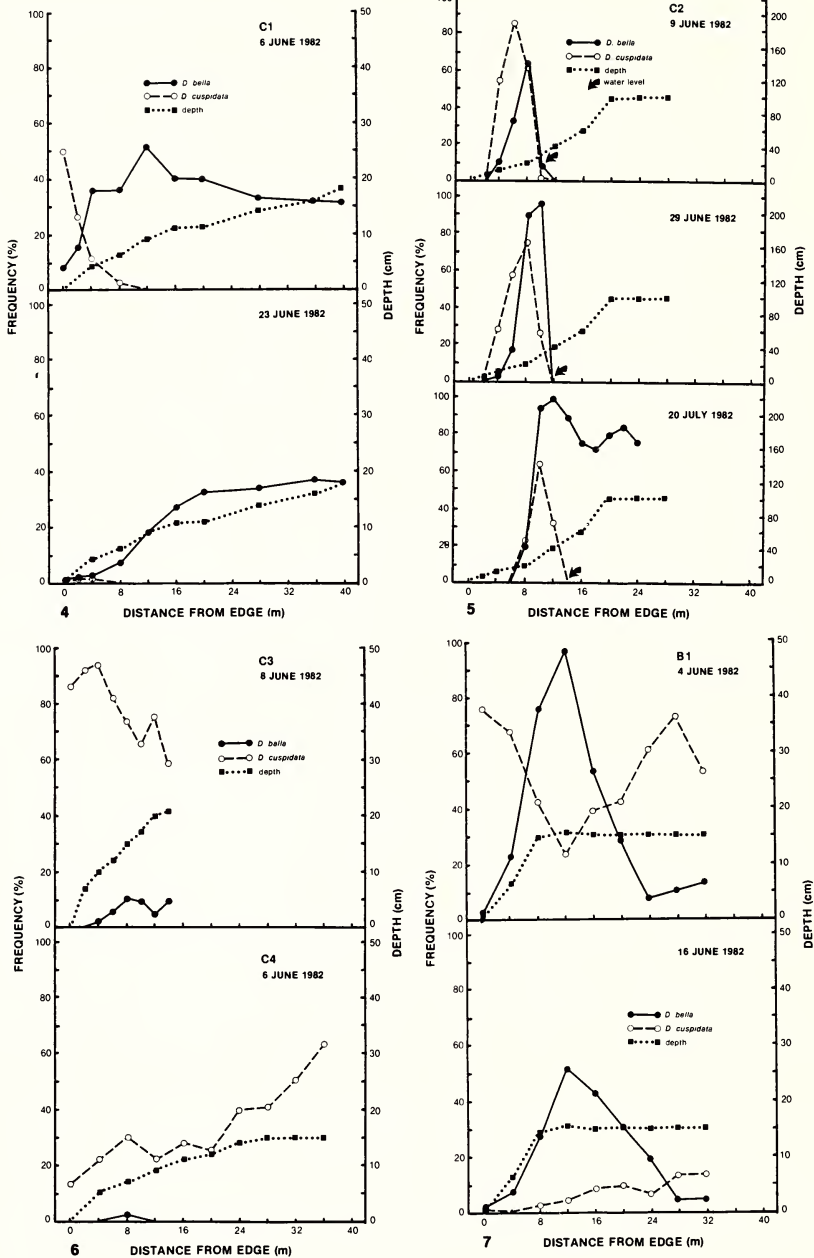
FIGS. 4–7. Flowering frequency of *Downingia bella* and *D. cuspidata* with pool depth at different distances from the edge of the pool. 4. Pool C1. 5. Pool C2. 6. Pools C3 and C4. 7. Pool B1.

highest frequency on the periphery. Pure stands of *D. bella* were observed in the center of pools B6, C1, and C2 after the last frequency measurements were taken. The most peculiar distribution pattern of all the pools was exhibited in pool B1, where *D. cuspidata* was distributed in a bimodal pattern with *D. bella* in a complementary unimodal pattern (Fig. 7). In general, however, flowering frequency of *D. bella* was correlated positively (r = +0.79) with pool depth, whereas frequency of *D. cuspidata* was correlated negatively (r = −0.86). Flowering frequency of *D. cuspidata* in pool C4 was correlated positively with pool depth, but individuals of *D. cuspidata* composed 99.6% of *Downingia* in this pool (Table 1). Plant density was correlated positively with flowering frequency for both *D. bella* (r = +0.91) and *D. cuspidata* (r = +0.92). Highest mean densities for *D. bella* and *D. cuspidata* were 356 and 406 plants/m², respectively.

*Flowering phenology.* Peak flowering periods for *D. bella* and *D. cuspidata* were positively correlated with pool desiccation dates (r = +0.94 and +0.89, respectively). Peak flowering of both species was delayed in vernal pools that had desiccation dates later in the season (Fig. 8). Peak flowering periods of the study species were segregated temporally at each pool (Fig. 8). The peak flowering period of *D. bella* usually occurred 2–4 weeks after the peak period for *D. cuspidata.* The first vernal pools to dry up in the 1982 season were pools B3, B7, and C4 (Fig. 8). *Downingia bella* was absent in pools B3 and B7 and nearly absent in pool C4. These pools appeared to be the shallowest pools. The last pools to desiccate were the deepest (pool B5) and the largest (pool C2). Dense stands of *D. bella* were observed flowering above water approximately 0.5 m deep during July in pools B6 and C2 (Fig. 5). *Downingia cuspidata* was not observed flowering while it was still in the open water zone.

*Morphology. Downingia bella* had significantly higher mean values (p < 0.01 or p < 0.001) for all seven morphological characters measured in comparison with *D. cuspidata* (Table 2). Plant height, and leaf, ovary, and corolla lengths, were more than 1.5 times larger in *D. bella.* Both species had numerous flowers per plant, with means of 9.1 and 6.5 for *D. bella* and *D. cuspidata,* respectively. The proportion of total flowers that were mature and open was 35% for *D. bella* and 43% for *D. cuspidata.*

*Pollination. Downingia bella* was visited only by hymenopterans. Principal visitors were *Bombus californicus* and *B. sonorus* (Table 3). *Downingia cuspidata* was visited by insects of several families (Table 3). The most common were *Syrphus* sp., a species of Calliphoridae, *Plebejus acmon acmon,* and *Vanessa virginiensis.* Visitors usually landed on the lower lobes of the corolla and appeared to
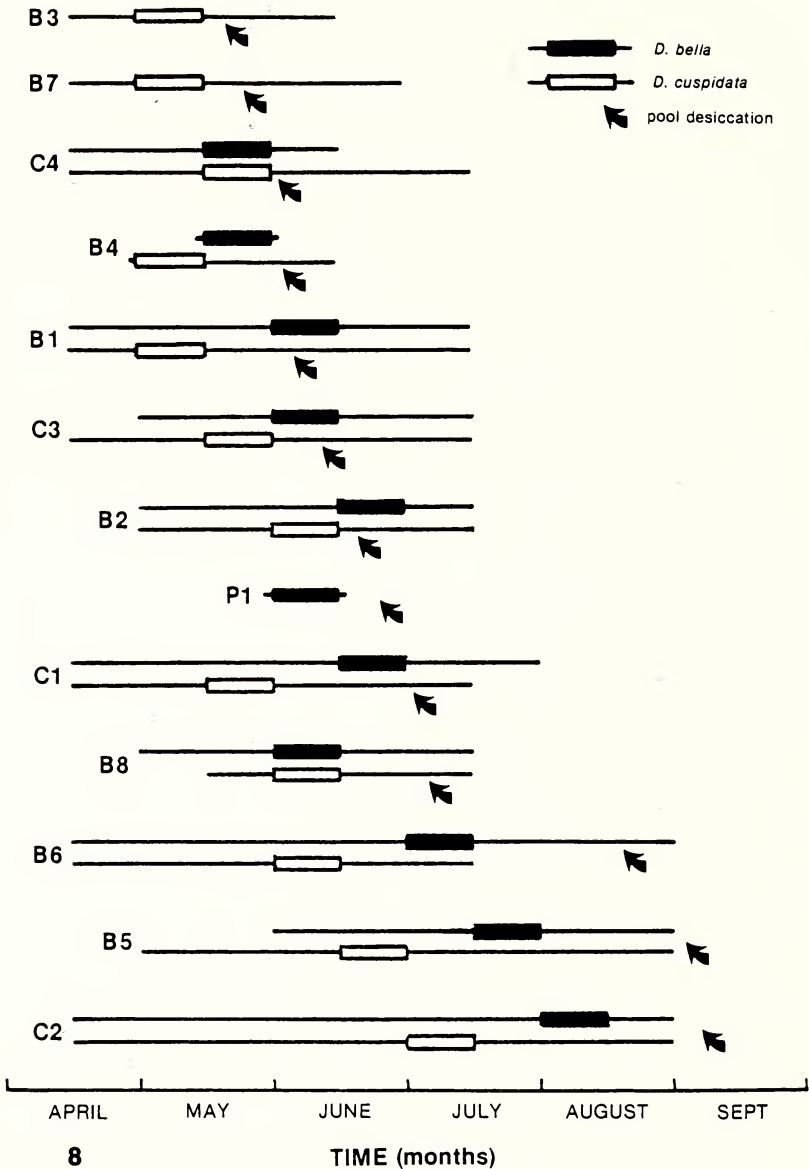
8 TIME (months)

FIG. 8. Flowering phenologies for *Downingia bella* and *D. cuspidata* in 13 vernal pools of the Santa Rosa Plateau Preserve. Rectangles represent the peak flowering periods. Arrows show pool desiccation dates.

probe for nectar inside the corolla tube. Neither species of *Bombus* was observed visiting *D. cuspidata* even though *D. cuspidata* was abundantly present.

<div align="center">DISCUSSION</div>

The differences demonstrated in distribution, flowering phenology, morphology, and pollinators of *D. bella* and *D. cuspidata* indicate that the two species occupy different niches. The main parameter of niche partitioning demonstrated was that of spatial segregation. Certain characteristic vernal pool species segregate into distinct zones or gradually change along the pool gradient (Lin 1970, Kopecko and Lathrop 1975, Schlising and Sanders 1982, Holland and Jain 1984, Zedler 1984). Species segregation usually is attributed to the gradual physical differences found between the extremes of the center of a pool and the adjacent higher grounds (Lathrop 1976, Linhart 1976, Holland and Jain 1984, Zedler 1984). The center of the pool has greater water availability and soil moisture stability when compared to the periphery. Species adapted to wetter environments are restricted to the deeper, more central areas of the pool. Conversely, species that can withstand greater variation in moisture conditions are often found in zones closer to the periphery of the pool.

Observations from our study indicate that *D. bella* requires a wetter, more stable niche than *D. cuspidata,* which perhaps accounts for the niche partitioning of the species. Two results demonstrate that the distribution of *D. bella* is limited by moisture: 1) flowering frequency of *D. bella* was correlated positively with pool depth; 2) *D. bella* was absent in the pools that desiccated earlier in the season. Also, Martin (1984) reported that percent germination of *D. bella* seeds was significantly higher in moister conditions. Lathrop (1976) found that the only soil characteristic of vernal pools that correlated with plant zonation was soil moisture. Moisture also seems to be the limiting factor in the distribution of *D. bella* between and within the vernal pools of the Santa Rosa Plateau Preserve.

*Downingia cuspidata,* like *D. bella,* is normally restricted to vernal pools. *Downingia cuspidata,* however, occupies a drier, more unpredictable niche. *Downingia cuspidata* was confined to the vernal pool because of moisture requirements, but was correlated negatively with pool depth. In pools where both species were sympatric, *D. cuspidata* was absent in the central areas of these pools.

Conceivably, physical factors other than moisture could exclude *D. cuspidata* from the centers of these pools. Lathrop (1976) reported that soil pH is more alkaline in the center of pool C2. The soil where *D. cuspidata* typically occurs in pool C2, along the periphery and outer zone of the pool, had a pH of 5.7, whereas the center area of the pool, where *D. bella* is more frequent, had a pH of 6.7. *Downingia*

TABLE 2. MORPHOLOGICAL CHARACTERS (MEAN ± S.D.) OF *Downingia bella* AND *D. cuspidata* FROM TWO VERNAL POOLS OF THE SANTA ROSA PLATEAU PRESERVE, CALIFORNIA. Plants were sampled in areas of each pool where the two species were sympatric. All morphological characters were significantly different (p < 0.01 or p < 0.001) between the two species. n = number of individuals sampled.

| Species | Pool | n | Morphological characters | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Plant height (cm) | Leaf length (mm) | Ovary length (cm) | Sepal length (mm) | Corolla tube length (mm) | Number of flowers/plant | Number of open flowers/plant |
| *D. bella* | B6 | 40 | 30.0 ± 6.6 | 10.5 ± 15.2 | 5.7 ± 1.0 | 5.6 ± 0.7 | 5.0 ± 0.3 | 11.6 ± 7.7 | 3.8 ± 2.0 |
| | C2 | 40 | 23.3 ± 5.0 | 12.0 ± 16.6 | 5.0 ± 0.9 | 5.9 ± 0.9 | 5.1 ± 0.3 | 6.5 ± 5.3 | 2.6 ± 1.7 |
| | $\bar{x}$ = | | 26.6 ± 5.8 | 11.3 ± 15.9 | 5.4 ± 1.0 | 5.8 ± 0.8 | 5.1 ± 0.3 | 9.1 ± 6.5 | 3.2 ± 1.9 |
| *D. cuspidata* | B6 | 31 | 19.9 ± 5.2 | 6.7 ± 3.9 | 3.5 ± 0.7 | 4.4 ± 0.7 | 3.4 ± 0.5 | 6.5 ± 2.5 | 2.7 ± 1.3 |
| | C2 | 31 | 14.2 ± 2.2 | 7.1 ± 1.2 | 2.8 ± 0.5 | 3.7 ± 0.5 | 3.1 ± 0.2 | 6.4 ± 3.3 | 2.8 ± 1.4 |
| | $\bar{x}$ = | | 17.1 ± 3.7 | 6.9 ± 2.6 | 3.2 ± 0.6 | 4.1 ± 0.6 | 3.3 ± 0.4 | 6.5 ± 2.9 | 2.8 ± 1.4 |

TABLE 3. INSECTS OBSERVED VISITING FLOWERS OF *Downingia bella* AND *D. cuspidata* IN VERNAL POOLS OF THE SANTA ROSA PLATEAU PRESERVE, CALIFORNIA. Listed by family, and by genus and species when known. * = fewer than 25 individuals. ** = more than 25 individuals.

| Plant species | Insect visitors | Abundance |
|---|---|---|
| *D. bella* | Hymenoptera | |
| | Anthophoridae | * |
| | Apidae | |
| | *Apis mellifera* | * |
| | *Bombus californicus* | ** |
| | *B. sonorus* | ** |
| | Halictidae | |
| | *Halictus* sp. | * |
| *D. cuspidata* | Coleoptera | |
| | Chrysomelidae | |
| | *Diabrotica undecimpunctata* | * |
| | Coccinellidae | |
| | *Coccinella california* | * |
| | *Hippodamia convergens* | * |
| | Diptera | |
| | Calliphoridae | ** |
| | Syrphidae | |
| | *Syrphus* sp. | ** |
| | Tabanidae | |
| | *Chrysops* sp. | * |
| | Tachinidae | * |
| | Hymenoptera | |
| | Apidae | |
| | *Apis mellifera* | * |
| | Halictidae | |
| | *Halictus* sp. | * |
| | Vespidae | |
| | *Polistes fuscatus aurifer* | * |
| | Lepidoptera | |
| | Hesperiidae | * |
| | Lycaenidae | |
| | *Plebejus acmon acmon* | ** |
| | Nymphalidae | |
| | *Vanessa virginiensis* | ** |
| | Pieridae | ** |

*bella* is known to be an alkali-tolerant species (Luckenbach 1973, Holland and Jain 1977, 1984). Water pH can also vary in vernal pools of different size. Lin (1970) reported that water pH in Solano County vernal pools ranged from 6.6–6.85 and that water in the smaller pools was more acidic. Thus, exclusion of *D. cuspidata* from the central areas of the deeper, larger pools may be due to differences in pH.

The role of competitive exclusion also must not be overlooked because it is known to play a role in plant zonation of vernal pools

(Linhart 1976, Ornduff 1976). Plant frequency of *D. cuspidata* was correlated negatively with pool depth in these pools containing both species, but a positive correlation was noted in pool C4 where *D. bella* was virtually absent. *Downingia cuspidata* may not compete well with *D. bella* or species associated with *D. bella* in the centers of the deeper pools. The pure stands of *D. bella* in the centers of pools B6, C1, and C2 were associated with dense stands of perennial *Eleocharis* spp. *Eleocharis* spp. were very sparse in pools B1 and B5 where *D. cuspidata* occurred at high frequencies in the central, deeper sections. Holland and Jain (1977) and Zedler (1984) also reported an increase in cover of *D. cuspidata* towards the center in pools at Rancho Seco and Kearny Mesa, respectively. Unlike findings in the present study, *D. bella* increased in cover along with *D. cuspidata* in the Rancho Seco pools. No *Eleocharis* spp. occurred at Rancho Seco, but they were infrequent at Kearny Mesa. Holland and Jain (1984) calculated depth preferences for 35 vernal pool species, including *D. bella* and *D. cuspidata. Downingia cuspidata* had a greater depth preference (11.1 cm) than *D. bella* (7.7 cm), which is contradictory to the results of this study. Most of the pools reported by Holland and Jain (1984), however, were much shallower ($\bar{x} = 17$ cm) than those in the present study ($\bar{x} = 53$ cm). Perhaps *D. cuspidata* is relatively scarce in the central portions of the deeper pools on the Santa Rosa Plateau because it apparently does not compete well with the perennial *Eleocharis* spp. due to its relatively small size. *Downingia bella* may be able to compete with *Eleocharis* in this central region, however, due to its larger size.

The temporal segregation of peak flowering periods observed for *D. bella* and *D. cuspidata* in the vernal pools of the Santa Rosa Plateau Preserve indicates niche partitioning between the species. Temporal segregation, however, appears to be an artifact of pool desiccation rather than due to genetically determined factors. Peak flowering periods were correlated positively with desiccation dates. Pools that retained water longer had peak flowering periods later in the season. The earlier desiccation around the periphery of the pool appeared to cause *D. cuspidata* to flower first. Competition for pollinators is decreased when flowering periods of the species are separated (Heinrich and Raven 1972).

Insect species observed visiting *D. bella* and *D. cuspidata* also demonstrate niche partitioning. The most important pollinators of *Downingia* are species of Hymenoptera, Diptera, and Coleoptera (Weiler 1962, Thorp 1976). The results of our study support this statement. Weiler (1962) reported some of the same species of insects observed in the present study as potential pollinators of *Downingia*. It was difficult to determine which species was the primary pollinator for *D. cuspidata*. Syrphid flies are thought to be pollinators for *D. concolor* (Weiler 1962, Linhart 1972) and could be primary polli-

nators of *D. cuspidata* because many were observed visiting this species. The primary pollinators of *D. bella* appeared to be *Bombus californicus* and *B. sonorus.* Martin (1984) reported that the mean corolla throat diameter of *D. bella* ($\bar{x}$ = 0.29 cm) was significantly larger than *D. cuspidata* ($\bar{x}$ = 0.17 cm), which would accommodate the larger *Bombus* pollinators. Both *Bombus* species apparently frequent *D. bella* equally and may be in competition for the same food source. Resource partitioning in *Bombus* on the same species is common (Morse 1977, Inouye 1978). *Bombus californicus* and *B. sonorus* showed flower constancy. Bumblebees are sensitive to UV, blue-violet, and yellow light (Macior 1978) and *Downingia* corollas reflect all three wavelengths, which makes them especially attractive to bumblebees. Possibly *B. californicus* and *B. sonorus* are capable of distinguishing between the two species by the corolla throat pattern (Martin 1984). Although bees orient to UV cues on flowers (Jones and Buchmann 1974) and bumblebees often exhibit flower constancy (Free 1970, Heinrich 1976), Weiler (1962) observed that *Bambus* spp. visited both *D. bicornuta* and *D. cuspidata* indiscriminantly.

Niche partitioning of *D. bella* and *D. cuspidata* was demonstrated by differences in the following: 1) *D. bella* occupied the deeper, central areas of the pools, whereas *D. cuspidata* was found around the periphery; 2) *D. bella* had peak flowering periods 2–4 weeks later than *D. cuspidata*; 3) *D. bella* was significantly larger than *D. cuspidata* for seven morphological characters; and 4) *D. bella* was pollinated primarily by *Bombus californicus* and *B. sonorus,* whereas *D. cuspidata* was pollinated by much smaller and more diverse insect species.

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# LETTERS

Dear Editor:

In a recent article by R. Becking (Madroño 33:175–181, 1986), *Hastingsia bracteosa* (=*Schoenolirion bracteosum*) is cited as a species listed as endangered by the U.S. Fish and Wildlife Service. In fact, *H. bracteosa* is merely a *candidate* for such status according to the reference given by Dr. Becking (USFWS, Federal Register 45:82479–82569, 1980). While this may seem a minor point, there are tremendous legal differences between formally listed taxa and those under consideration for listing. It is therefore imperative that we clearly and accurately define the status of rare species discussed in our papers. Powell and Howard (Madroño 25:59, 1978) emphasize the importance of addressing the subjects of rarity and potential endangerment of plant species in published research. In echoing their plea, I would respectfully add that we choose our wording carefully in order to avoid further complication of an intricate land management issue.

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Dear Editor:

In reading the recent article describing *Hastingsia atropurpurea* (Madroño 33:175–181, 1986), the author, Rudolf Becking, erroneously reported that *H. bracteosa* was "an endangered species", citing a notice published by the U.S. Fish and Wildlife Service in the *Federal Register* (45:82479–82569, 1980). However, this notice only indicated that *Schoenolirion bracteosa* was a category 1 "candidate" species (taxa for which the Service currently has on file substantial information on biological vulnerability relating to autecology and distribution and threat(s) to support the appropriateness of proposing to list the taxa as endangered or threatened species), not an "endangered" species under the Endangered Species Act of 1973. The generic epithet was changed to *Hastingsia* in the *Federal Register* (48:53651) in 1983. The most-recent notice in the *Federal Register* (50:39554, 1985) reaffirmed the 1983 notice. Copies of all three notices may be obtained from my office upon request.

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